

Leaf Phenology and Trunk Growth of the Deciduous Tree Fern *Alsophila firma* (Baker) D. S. Conant in a Lower Montane Mexican Forest

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ABSTRACT.—Tree ferns are often regarded as evergreen, non-seasonal, slow-growing plants of tropical forests. However, several species possess seasonal leaf phenology patterns and seasonal differences in growth rates. To investigate the environmental triggers which influence leaf phenology and to measure trunk growth rates, we studied a population of *Alsophila firma* at Las Cañadas, Huatusco, State of Veracruz, Mexico. We measured leaf traits monthly for 26 mo and trunk height at the beginning and end of the study. *Alsophila firma* showed a unique seasonal pattern of leaf phenology, shedding its leaf pinnules when they are yellow or still green during the wet season, and 50–70% of plants stay leafless for at least 1 mo, after which strongly asynchronous leaf flush occurs. This phenological pattern may be of advantage to evade higher herbivore pressure of the wet season and to benefit from higher light levels in the understory during the dry season when a proportion of canopy trees are leafless. The trunks had a mean height of 2.46 ± 0.16 m, a mean leaf number of 5.2 ± 0.27 ($n = 169$), and 25% of the plants were fertile. Mean annual trunk growth was 17.1 ± 0.85 cm. Based on this trunk growth rate, the tallest tree ferns (>10 m) are at least 60 yr old.

KEY WORDS.—age estimate, *Alsophila firma*, *Cyatheaceae*, deciduous, leaf life span, Mexico, trunk growth, phenology, seasonality, tree ferns

The tree fern families of Cibotiaceae, Cyatheaceae and Dicksoniaceae together comprise over 640 species worldwide (Smith *et al.*, 2006) of which approximately 180 species occur in the neotropics (Tryon and Tryon, 1982). The neotropical center of diversity extends from the mountain ranges of Costa Rica and Panama to the Andes of Bolivia and Venezuela, with 40–50 species per country. In Mexico, there are 18 species of tree ferns (Mickel and Smith, 2004).

Tree ferns are striking elements of the tropical forest vegetation and have attracted attention of ecologists for decades (Arens, 2001; Ash, 1987; Bittner and Breckle, 1995; Conant, 1976; Seiler, 1981, 1984; Tanner, 1983). However, little is understood about their leaf phenology and the environmental triggers which influence leaf emergence, leaf fall and fertility. Reported trunk growth rates vary among species preventing common estimates of their age (Bittner and Breckle, 1995; Chiou *et al.*, 2001; Durand and Goldstein, 2001; Seiler, 1981; Tanner, 1983). Bittner and Breckle (1995) reported that leaf production of two Costa Rican species (*Alsophila polystichoides* H. Christ and *Cyathea nigripes* (C. Chr.) Domin) is seasonal and that the plants were leafless during a period of the year, however they did not observe if the leaves of these species

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withered as a passive response to dryness or if they were actively shed. Because their observations were taken every 3 to 4 mo, the causal relationship between environmental conditions and leaflessness were unclear.

To understand the correlation between seasonal climatic conditions and the pattern of leaf phenology, and to determine annual trunk growth and predict trunk age, we chose to study *Alsophila firma* (Baker) D. S. Conant, a common species in the State of Veracruz, Mexico. The trunks of *A. firma* are exploited as construction material and the root mantle (Span. 'maquique') is used as substrate for orchid cultivation. Because of intensive commercial use, natural populations have been severely damaged and, as a consequence, the species has been protected by Mexican laws (SEMARNAT, 2002). Moreover, tree ferns are important hosts for native epiphytes (Cortez, 2001; Moran *et al.*, 2003), and some species including *Trichomanes capillaceum* are obligate on tree fern trunks and commonly found growing on *A. firma* (Mehltreter *et al.*, 2005). Despite its wide geographic range from Mexico to Panama and Ecuador (Mickel and Smith, 2004), abundance, commercial use, conservation status, and its significance as host for epiphytes, there does not exist ecological field data.

We investigated the frequency of trunk size classes, trunk growth and leaf phenology of a natural population of *Alsophila firma* to determine whether leaf traits correlate with monthly means of temperature and precipitation, and to estimate the age of individuals.

MATERIALS AND METHODS

The study site "Las Cañadas" (19°10'35" N, 96°58'19" W) is a private reserve with 118 ha of lower montane forest, located at 1340 m elevation on the eastern slope of the Sierra Madre Oriental near the city of Huatusco, Veracruz, Mexico. The climate is warm with a wet season from May to October with average temperatures of 21.3°C and 271 mm monthly rainfall, and a dry season from November to April with 18.2°C and 54 mm monthly rainfall (averages of 56 yr, second nearest weather station Huatusco). The lower montane forests grow on andosolic soils along humid river gorges. Dominant canopy forest trees are *Clethra mexicana* DC., *Juglans pyriformis* Liebm., *Quercus insignis* M. Martens & Galeotti, *Q. leiophylla* A. DC., and *Q. xalapensis* Bonpl. Three tree fern species are conspicuous elements of the understory: *A. firma*, *Cyathea bicrenata* Liebm., and *C. divergens* Kunze var. *tuerckheimii* (Maxon) R. M. Tryon, only the first being common.

In July 2003, we tagged 169 living, undamaged trunks along a 300 m section of a forest trail. In April 2004 and May 2006, height was determined on the labeled trunk side as the distance from soil to the top of the small unexpanded crosiers. Larger trunks were measured with a 12 m telescopic measure rod, and smaller trunks (< 2 m height) with a flexible tape. Trunks were grouped into 0.5 m size classes. For each size class growth rate was averaged and trunk age estimated, assuming that trunk age is directly proportional to size. Trunk age of each size class was defined as the sum of the age of all preceding size classes. In comparison to the often used mean trunk growth of the entire population,

the following equation is independent from the number of individuals in each size class:

$$\text{Trunk age}_{\text{sizeclass}} = c_0 + \sum_{i=0.5}^{\text{sizeclass}} \frac{0.5m}{g_i}$$

where g_i is the mean annual trunk growth per size class i . The constant c_0 stands for the age of the trunkless 0 m size-class and was set to a mean of 1 yr, because our smallest trunkless sporophytes from April 2004 had initiated trunk growth before May 2006.

Plant fertility (presence of spore-bearing fertile leaves) was observed with binoculars and leaf number was counted for all plants in May 2006.

Leaf phenology was studied on a subset of 39 randomly selected trunks of less than 2 m height to allow working without a ladder, and to avoid damaging the leaves during measurements. We assumed that leaf phenology does not differ on larger plants for which we have observed the same leaf fall pattern as in smaller plants, although they possess a larger number of leaves. From July 2003 to September 2005, we counted the number of fertile and sterile green leaves, and the number of new and dead leaves monthly. Each leaf was labeled. Leaf length was measured with a flexible tape on the adaxial (upper) side, from the leaf insertion, where the petiole meets the trunk, to the leaf tip. Total leaf growth is the length added to all growing leaves during one month (Mehltreter, 2006). Leaves with an expanding crosier at the tip (but without expanded lamina) were noted as new when discovered for the first time. Leaves with partially or completely expanded lamina were considered as green. Leaves were noted as dead the first time when no green lamina remained. Generally the rachis was still attached to the plant. Leaves with damage >50% (by wind or herbivory) during the first two months were identified, and leaf life span was calculated independently for damaged, undamaged and all leaves together. Leaf life span was recorded for each leaf as the time between the first observation date as a crosier and the date when the leaf was noted as dead. Six of 264 leaves, for which one date was not observed, were discarded from this calculation. Mean leaf length was calculated for each individual including all completely expanded leaves with undamaged apices, and then averaged for the population. Repeated measures Analysis of Variance (RM-ANOVA) and Spearman ranked correlation analysis (r_s) were used to test for correlations between leaf traits, trunk height and monthly means of temperature and precipitation from the nearest weather station (Chapingo, Huatusco). A time series was applied to investigate weather climate data of the same month, the preceding month or two months earlier were more strongly correlated with phenological data. Data were analyzed with SigmaStat (2004). Results are given as means \pm 1 SE.

RESULTS

Population structure.—All 0.5 m size classes up to 8.5 m trunk height were represented in the studied population, with smaller size classes being more

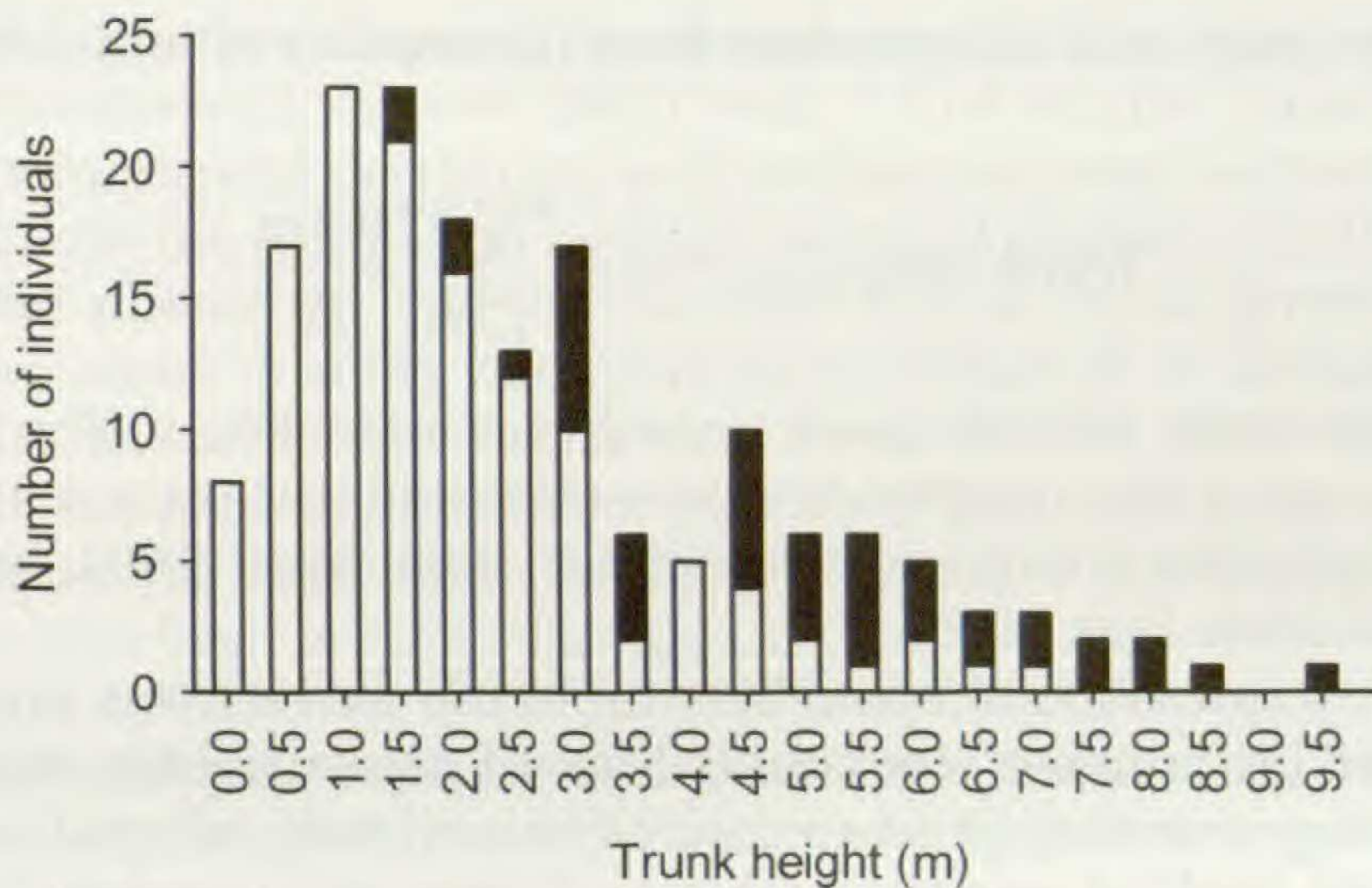


FIG. 1. Frequency of 0.5 m size classes of *Alsophila firma* ($n = 169$). Fertile plants (black), sterile plants (white).

frequent, and a higher proportion of fertile plants within larger size classes (Fig. 1). Twenty-five percent of the population was fertile. The tree ferns had a mean height of 2.46 ± 0.16 m, and a mean leaf number of 5.2 ± 0.27 ($n = 169$). Mean leaf number was not significantly correlated with trunk height.

Leaf phenology.—The subset of 39 plants (only one fertile) for the phenological study, had a mean number of 2.6 ± 0.22 green leaves during the observation period, with a strongly seasonal leaf turnover, repeating a similar phenological pattern during both observation years (Fig. 2a). At the beginning of the wet season in May, leaf mortality increased significantly, followed one month later by an increase in leaf production. From June to July the number of green leaves reached its minimum (1.54 ± 0.08 leaves, Fig. 2a), when 60% of all plants (51% in 2004, 70% in 2005) were completely leafless for at least 1 mo (Fig. 3). Although the number of deciduous plants varied between the two observation years, differences were not significant ($\chi^2 = 5.514$, $p = 0.48$, $n = 39$).

Because 40% of the plants were leaf-exchanging (i.e. they formed new crosiers at the same time that old leaves were shed), the mean leaf number of the population never declined to zero (Fig. 2a). However, all plants produced new leaves synchronously in one flush from June to September. One-third of the plants also produced one (7 plants) or two leaves (6 plants) from October to May, contributing 7.2% of all observed leaves. New leaves expanded completely within 2 to 3 mo and the mean leaf number recovered its maximum again in September–October (3.5 ± 0.32), at the end of the rainy season (Fig. 2a). The plants had a lower mean leaf number in the wet season, when the complete leaf turnover occurs. Concurrent with this, the number of crosiers and dead leaves was highest during the wet season (Table 1).

Leaf production and leaf mortality were strongly correlated with monthly precipitation and monthly mean temperature, and may be triggered by both environmental parameters. A time series analysis reveals that only leaf

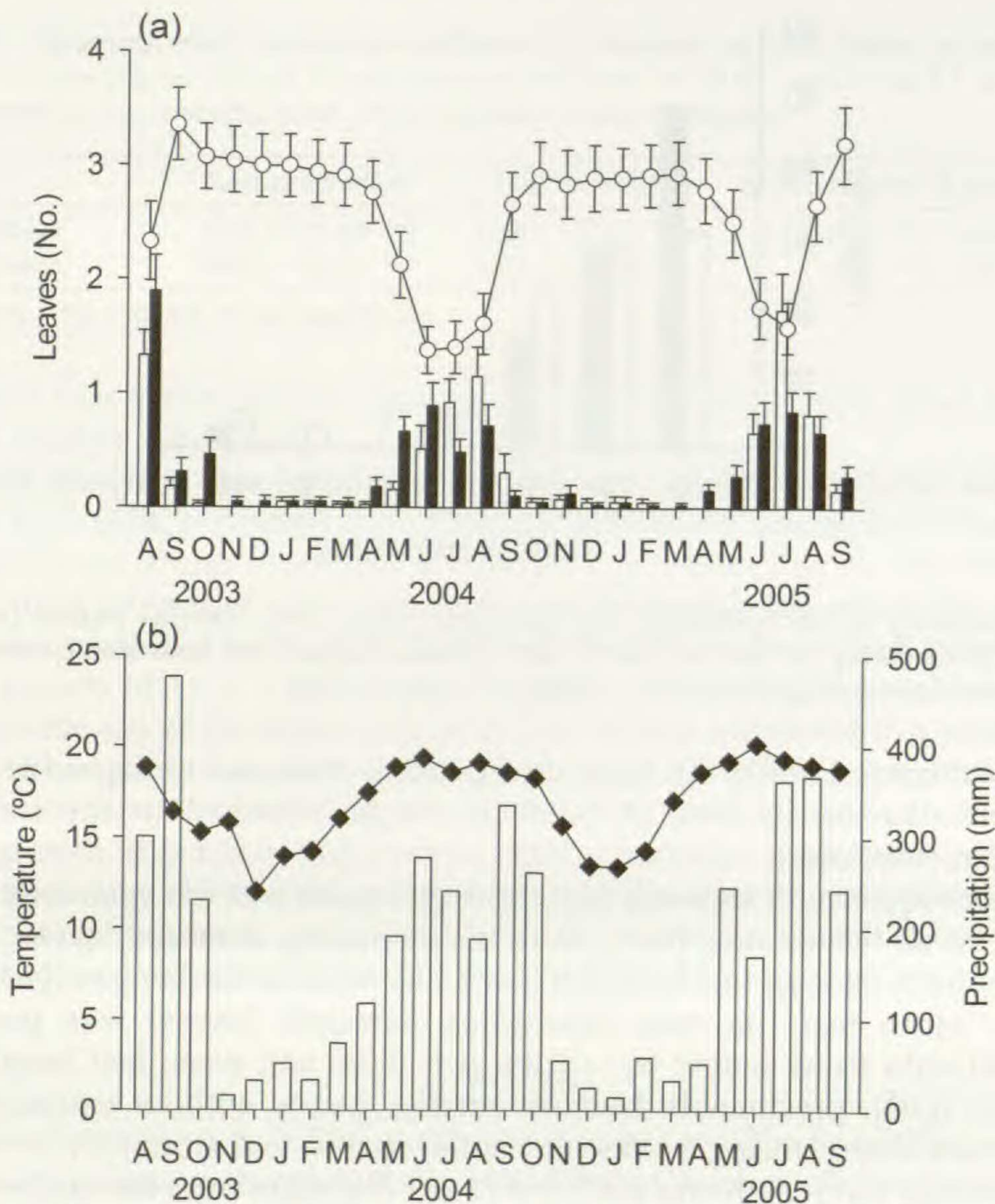


FIG. 2. (a) Leaf production (= crosiers, white columns), leaf mortality (black columns) and number of green leaves (white circles) of 39 randomly selected plants (< 2 m in trunk height) of *Alsophila firma*. Because crosiers develop slowly, they add to the number of green (expanded) leaves after at least a one-month delay. (b) Mean temperature (black diamonds) and precipitation (white columns) from August 2003–September 2005 (weather station Chapingo, Huatusco).

production (number of crosiers) may show a delayed response to temperature, because it is more strongly correlated with mean temperature of the preceding month (Table 2) rather than the same month. Although leaf production during the wet season 2005 was significantly higher than the year before (Table 1), chi-square analysis suggests that the duration of the leafless period did not change significantly between the two years of observation ($\chi^2 = 5.514$, $p = 0.48$, $n = 39$).

Alsophila firma sheds its leaf pinnules (blade segments of second order) during the wet season, when they are yellow or still green, i.e. they do not simply wither, but are abscised at an articulation at the costa (pinna midvein). In a further stage, the costae are abscised at the rachis, leaving a scar with a

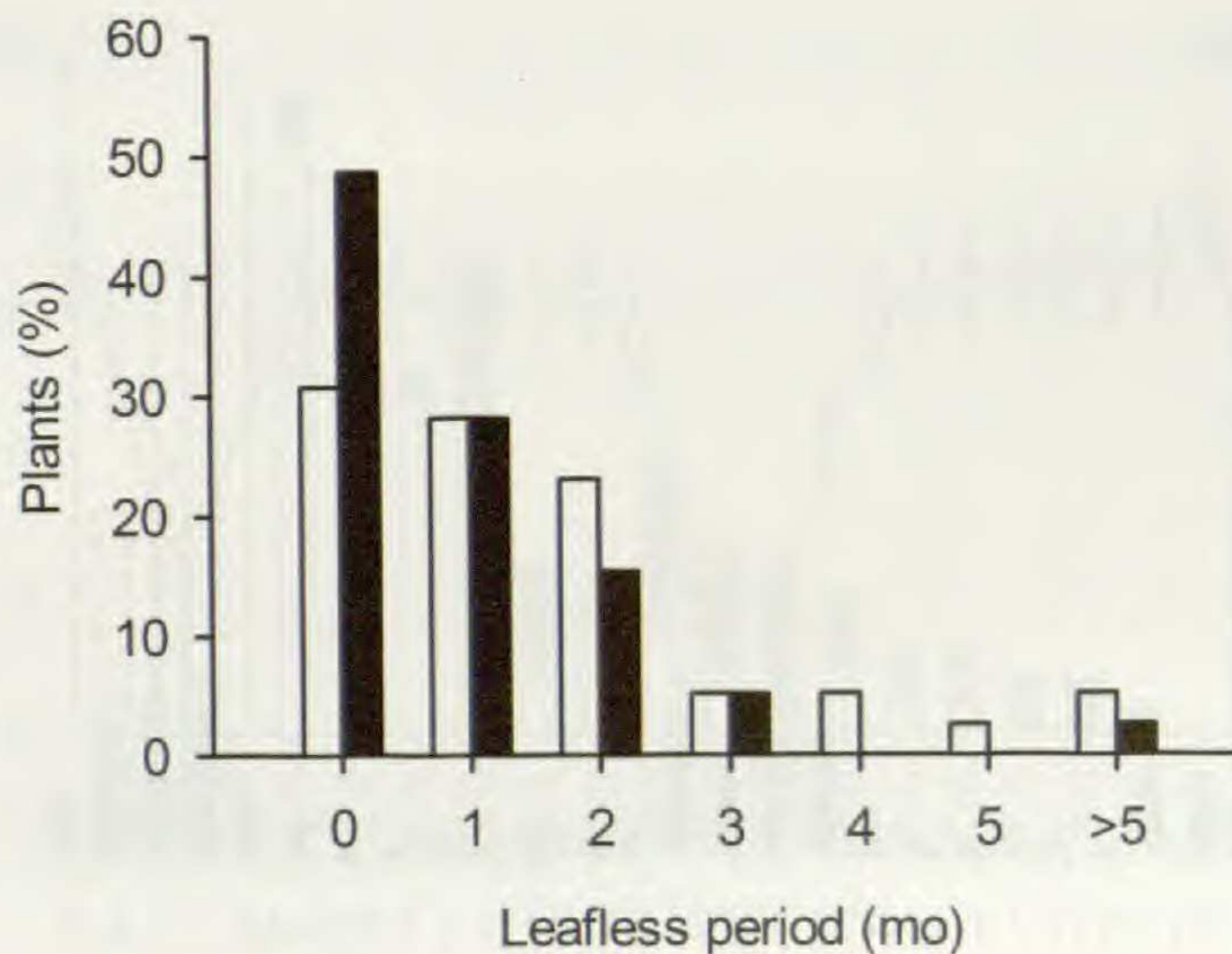


FIG. 3. Frequency of leaf exchanging and deciduous plants (with differing leafless period) of *Alsophila firma* during the wet seasons of 2004 (white columns) and 2005 (black). Differences between years were not significant ($\chi^2 = 5.514$, $p = 0.48$, $n = 39$).

central leaf trace. Finally the stipe (leaf petiole) dries and collapses or breaks irregularly, leaving its base of 5–10 cm length attached to the trunk (K. Mehlreter, pers. obs.).

As a consequence of seasonal leaf turnover, mean leaf life span was 10.0 ± 0.29 mo for all leaves, and 10.7 ± 0.19 mo excluding damaged leaves. Leaves with over 50% damage (8.5% of 258 leaves) by wind or herbivores lived 3.0 ± 0.66 mo. Mean leaf life span (excluding damaged leaves) was positively correlated with trunk height ($r_s = 0.34$, $p = 0.03$) and mean leaf length ($r_s = 0.34$, $p = 0.03$), presumably because smaller plants without extensive root systems and water storing trunks may suffer earlier leaf mortality.

The average leaf length was 2.57 ± 0.17 m. The plant with the largest leaves had a mean leaf length of 3.91 ± 0.04 m, while the plant with the smallest leaves had a mean leaf length of 0.58 ± 0.01 m. The mean leaf length was strongly correlated to trunk height (Fig. 4), with the logarithmic regression curve fitting better ($r = 0.91$) than the linear regression ($r = 0.82$). A logarithmic regression integrates the values of smaller plants better, and

TABLE 1. Seasonality of *Alsophila firma* at Las Cañadas montane forest in Veracruz, Mexico. Figures in columns are monthly rainfall and number of leaves per plant (Means \pm 1 SE). Letters indicate significant differences among seasons (RM-ANOVA, $n = 39$, $p < 0.05$).

Time	Season	Monthly rainfall (mm)	Leaf production	Leaf mortality	Mean number of green leaves
Nov 2003–Apr 2004	Dry	54	0.02 ± 0.01^a	0.07 ± 0.02^a	2.9 ± 0.27^a
May–Oct 2004	Wet	249	0.52 ± 0.05^b	0.49 ± 0.05^b	2.0 ± 0.18^b
Nov 2004–Apr 2005	Dry	39	0.04 ± 0.01^a	0.07 ± 0.02^a	2.9 ± 0.28^a
May–Sept 2005 *	Wet	278	0.68 ± 0.07^c	0.56 ± 0.06^b	2.3 ± 0.21^b

*October as missing value

TABLE 2. Spearman rank correlation-coefficient (r_s) between monthly means of leaf traits of *Alsophila firma* (Figure 2a) and climatic parameters (Figure 2b) at the same mo and 1 mo before (in parentheses) in the montane forest of Las Cañadas, Veracruz, Mexico.

	Leaf production	Leaf mortality	Mean number of green leaves
Temperature	0.56 ** (0.69 **)	0.80 ** (0.75 **)	-0.71 ** (-0.54 *)
Precipitation	0.65 ** (0.51 *)	0.69 ** (0.57 *)	-0.36 ^{ns} (-0.06 ^{ns})

* $p < 0.05$, ** $p < 0.005$, ^{ns} not significant

indicates that plants initiate substantial vertical trunk growth when mean leaf length reaches 1.5–2.5 m.

Trunk growth.—The trunk growth rate was weakly correlated with trunk height ($r_s = 0.39$, $p < 0.001$, $n = 169$), but differences among size-classes were not significant (Dunn's multiple comparison, $p < 0.05$, Fig. 5). Considering the mean trunk growth of each size class (see Methods), the age of the 6 m size class was projected to be 39.7 yr (Fig. 5). Based on the overall mean annual trunk growth of $17.1 \pm 0.85 \text{ cm}\cdot\text{yr}^{-1}$, plants of 6 m height would be 35.1 yr old, and the age of the tallest tree ferns (10 m) was estimated to a minimum of 60 y. Although the smallest fertile plant was 1.38 m tall, most fertile plants (90%) were over 2 m high (Fig. 1) and at least 12 yr old, based on mean annual trunk growth. It is likely that several years are needed from spore germination to the initiation of vertical trunk growth, and therefore the complete life cycle from spore germination, gametophyte development, and fertilization up to the time of spore production is longer than indicated by these estimates.

DISCUSSION

Population structure.—The study site appears to offer favorable conditions for growth and reproduction of *Alsophila firma*, because of the presence of all

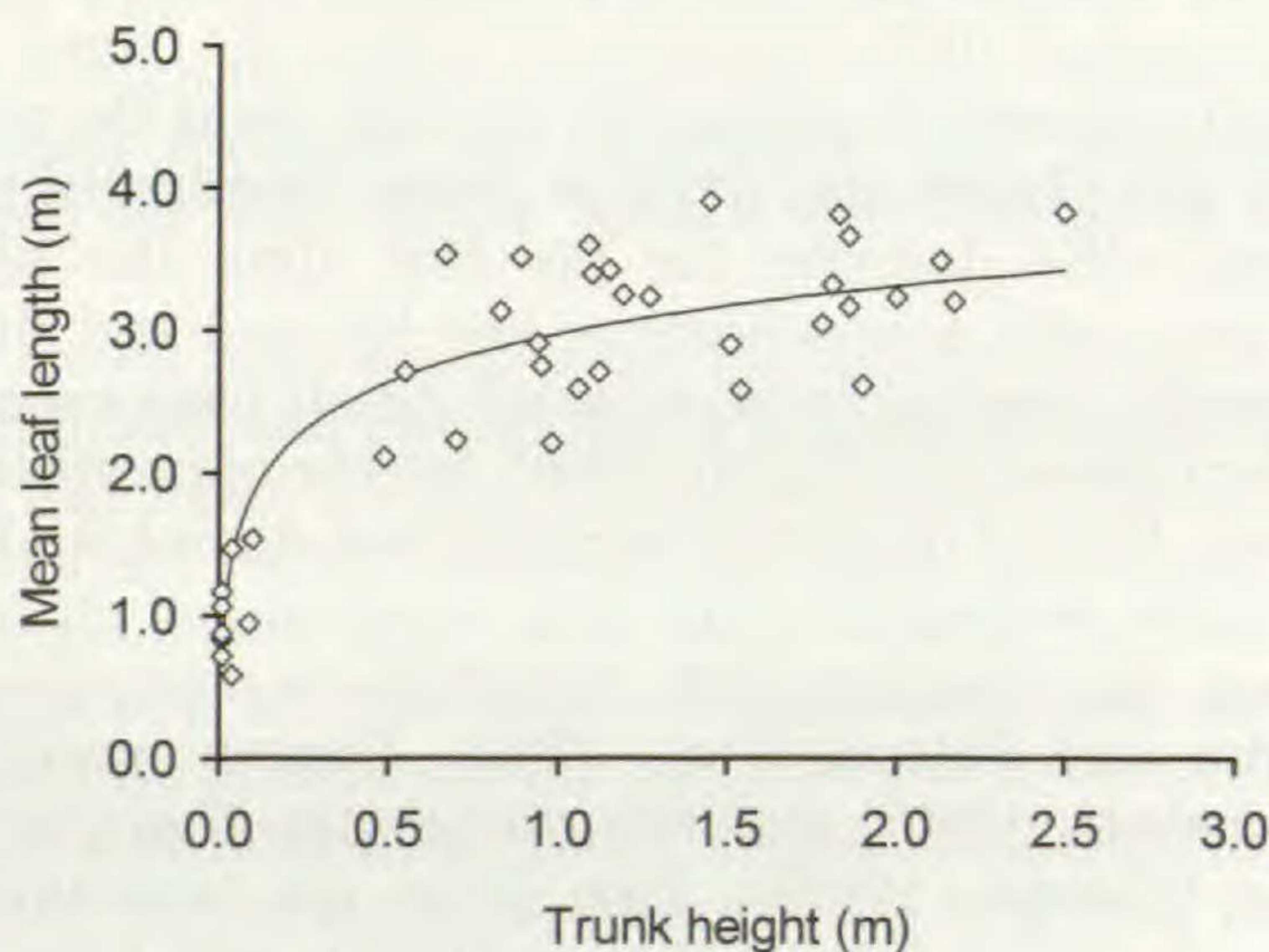


FIG. 4. Logarithmic regression ($y = -0.4921 \cdot \ln x + 2.977$, $r = 0.91$, $p < 0.001$) between trunk height and mean leaf length in *Alsophila firma* ($n = 39$).

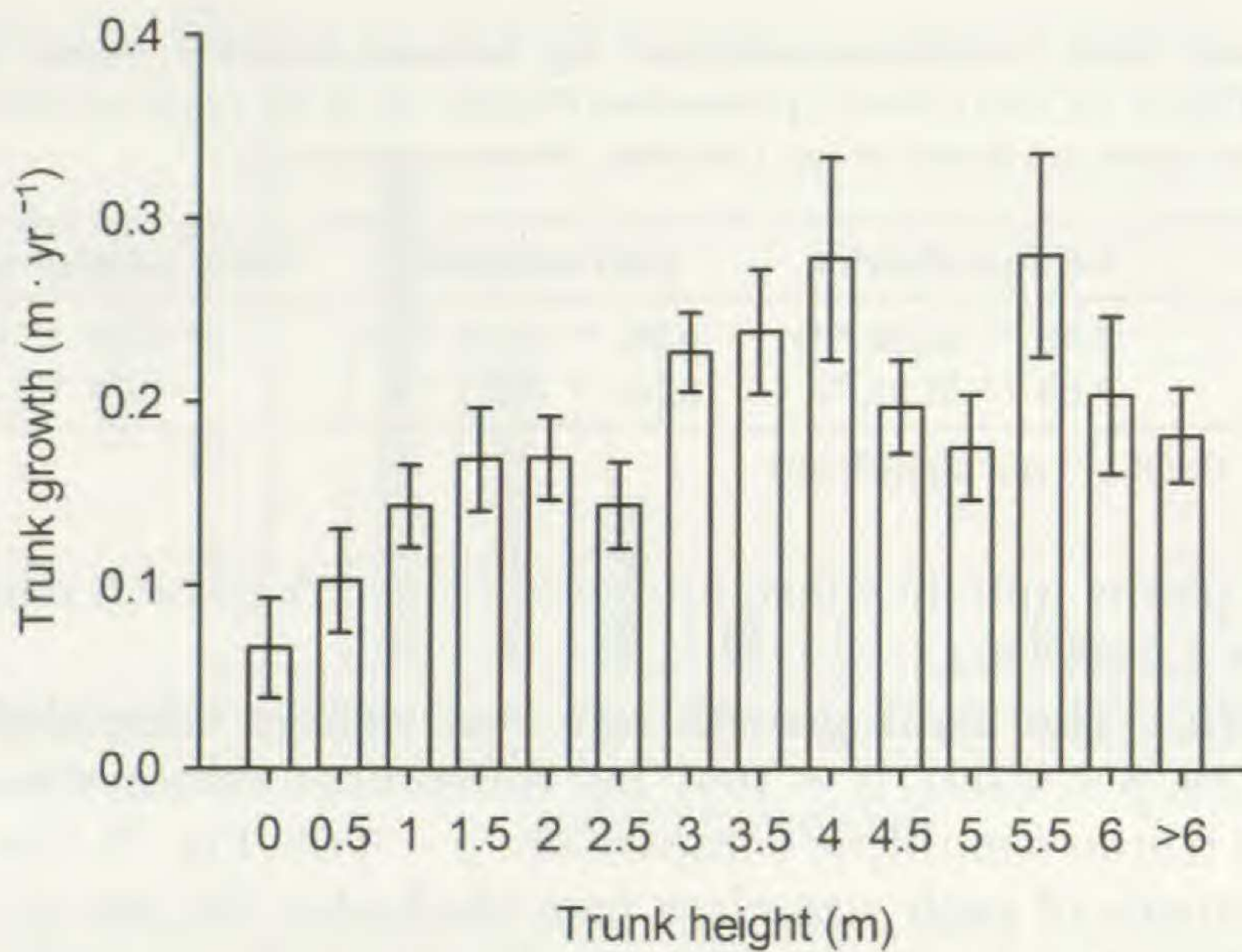


FIG. 5. Annual trunk growth rate of *Alsophila firma* ($n = 169$). Differences among 0.5 m size-classes were not significant (Dunn's multiple comparisons, $p < 0.05$). Means ± 1 SE.

size classes of up to 8.5 m, and the fertility of 25% of the population. Nagano and Suzuki (2007) found a similar population structure and 33% of population fertility in *Cyathea spinulosa* Wall. ex Hook. in Japan. However, their smallest size class was the most frequent (45%), similar to results from Tanner (1983) for *Alsophila auneae* (syn. *Cyathea pubescens*) in Jamaica (68%). In *A. firma*, we found low frequencies of the two smallest size classes (5% and 9%, respectively) that may indicate a restriction of available micro-sites for successful reproduction. Furthermore, we observed lower frequencies within 3.5–4.0 m size classes which may indicate a disturbance at the study site some 20–24 yr ago (based on the estimated annual mean trunk growth). Light seems to promote fertility because the relative percentage of fertile plants increased with height, and reached 100% fertility only within the largest size classes (> 7 m; Fig. 1), which succeed in getting full sunlight along the river bed. Fertile plants of smaller size classes may grow on better illuminated sites.

Leaf phenology.—We describe for the first time the phenology of a deciduous tree fern, with a synchronous leaf fall and leaf flush during the wet season. Generally, tropical ferns of humid forests were expected to possess a non-seasonal leaf phenology (Tryon, 1960), but the opposite has been shown for several species. Even if minimum temperatures do not fall below zero and soil water is available during the entire year, seasonal leaf phenology has been demonstrated (e.g. the mangrove fern *Acrostichum danaeifolium* Langsd. & Fisch. (Mehltreter and Palacios-Rios, 2003), *Danaea wendlandii* Rchb. f. (Sharpe and Jernstedt, 1990), and the rheophytic *Thelypteris angustifolia* (Willd.) Proctor (Sharpe, 1997)). Tree ferns are commonly considered evergreen, although Seiler (1981), Tanner (1983), and Bittner and Breckle (1995) have observed seasonal leaf production for different species in El Salvador, Jamaica and Costa Rica, respectively.

The deciduous leaf phenology of *A. firma* shedding its leaf pinnules unexpectedly during the wet season is not easily explained. Elliott *et al.* (2006) described three functional types of vegetative phenology for tropical trees: (a) deciduous with rain induced leafing, (b) light induced spring-flushing, and (c) drought induced leaf-exchanging species. Deciduous species shed their leaves in the early dry season and flush after the first rainfalls of the wet season. Spring-flushing trees expand new leaves synchronously during the dry season, because of the photoperiodic induction during the spring equinox and their access to subsoil water reserves (Rivera *et al.*, 2002). Leaf-exchanging species are confined to moist riparian sites, shed their old, mature leaves at the height of the dry season and replace them more or less immediately with new leaves. *Alsophila firma* does not fit in any of these phenological patterns. Although a deciduous species, it sheds the mature leaves at the beginning of the wet season and not during the dry season, but leaf mortality and leaf flush seem to be rain and temperature induced (Table 2). In contrast to light induced species, which flush in spring after vernal equinox, leaf flush in *A. firma* is three months delayed, but leafing is synchronous and might be induced by the longest photoperiod around summer solstice. If leaf emergence in *A. firma* was light induced, changes in annual rainfall patterns should not affect their timing. However, earlier rainfalls in March and April 2004 sped up leaf mortality and leaf flush in May 2004 (Fig. 2). Finally, *A. firma* inhabits riparian habitats within 30 m distance of the river bed, typical for leaf-exchanging species and new leaves developed soon after leaflessness. *Alsophila firma* cannot be classified as leaf-exchanging species though, because 60% of the plants remain leafless for at least one month during the wet season, when water availability would not be expected to be a limiting factor. Furthermore, leaf mortality was strongly correlated with increasing rainfall and temperature, which does not support the hypothesis of a drought induced leaf fall of old leaves, typical for leaf-exchanging species with poor stomatal control (Borchert, 2005). For these reasons, we conclude that *A. firma* has a unique leaf phenology, which we define as short-deciduous, characterized by rainfall (and temperature) induced leaf abscission and synchronous new leaf formation during the wet season, after a short period of at least 1 mo of leaflessness.

Elliott *et al.* (2006) reported unusual leaf flushes during the dry season in Asian monsoon forests and proved that soil water accessibility permits deep-rooting trees to leaf before the first rainfalls. Because *A. firma* does not shed its leaves during the dry season, water access seems an unlikely problem. Why then should these plants drop their leaves during the wet season? Water conducting efficiency of tree ferns is supposedly low in comparison to angiosperms, because of more narrow tracheids and fewer wide vessels in their xylem (Carlquist and Schneider, 2001). Higher temperatures during the wet season (May–Oct) may cause water stress in the large tree fern leaves, when water conduction cannot keep pace with increasing evapotranspiration rates, although there is enough soil water available. In support of this assumption, leaf mortality was strongly correlated with temperature (Table 2). Starch and

other nutrients can be stored along the entire length of the trunk (syn. *Nephelea mexicana*; Feldman and Nardi, 1973) until most crosiers are produced from June to August when growth conditions are best (high temperatures and rainfall). However, these new leaves need 2–3 mo for their expansion, and their leaf surface will not be exposed before August or September (Fig. 2). During the dry season (Nov–Apr), lower temperatures reduce water loss by evapotranspiration, and photosynthetic processes may benefit from more sunlight in the understory when deciduous canopy trees of the lower montane forest (50% at the study site) are leafless from November to February (Williams-Linera, 1997).

Although we may interpret satisfactorily the leaf fall pattern of *A. firma* as an environmental adaptation to assumed water stress during the hottest summer months, it is important to note that we have never observed similar traits in the other two coexisting tree fern species at the study site: *Cyathea bicrenata* and *C. divergens* var. *tuerckheimii*, both evergreen species with a continuous leaf production and leaf loss. These two species may possess more efficient water conduction or better stomatal control to avoid water stress, hypotheses that could be tested in further studies. Species of *Cyathea* which grow in open habitats rather than understory seem to tolerate the higher light intensity (D. Conant, pers. comm.) and do not drop their leaves. Their stems store some starch at the apex, but not along the entire length of the trunk as in *A. firma* (Feldman and Nardi, 1973). Synchronous leaf emergence is advantageous against insect herbivory (Aide, 1993; Lieberman and Lieberman, 1984; Rathcke and Lacey, 1985; van Schaik *et al.*, 1993). As the most common understory species, *A. firma* could be the favorite target for insects. However, when insects are more abundant during the wet season (Janzen, 1973; Wolda, 1988), *A. firma* may escape herbivory by its leaflessness. Indeed, we observed some crosiers of *A. firma* damaged by insects at the study site, and this damage shortened leaf life span significantly from 10 to 3 mo. In support of this hypothesis, *C. bicrenata* with continuous leaf emergence during the entire year seems to suffer more herbivore damage (K. Mehlreter, pers. obs.).

Trunk growth.—Our results confirm that *A. firma* exhibits typical growth rates and leaf numbers of a primary forest species. Trunk growth of tree ferns varies greatly among species and different habitats (Table 3). Even at the generic level there seems to be no common pattern. There are fast growing species in the genera *Alsophila*, *Cyathea* and *Sphaeropteris* (all Cyatheaceae), with the exception of the slow growing *Cibotium* (Cibotiaceae; Smith *et al.*, 2006)(Table 3). Trunk growth of tree ferns of secondary habitats in Costa Rica (*C. bicrenata*, syn. *C. trichiata*) increase four to eightfold in comparison to primary forest species. *Cyathea delgadii*, a species occurring in both habitats, accelerates its growth rate under sunny conditions fourfold to more than $80 \text{ cm}\cdot\text{yr}^{-1}$, and doubles its leaf number (Bittner and Breckle, 1995). Arens (2001) came to similar conclusions for *Cyathea caracasana*, a Colombian tree fern which occurs in several habitat types. *Cyathea caracasana* grew $4.8 \text{ cm}\cdot\text{yr}^{-1}$ in the forest understory and $16.8 \text{ cm}\cdot\text{yr}^{-1}$ in open habitat.

TABLE 3. Leaf traits of tree ferns from primary forests in order of increasing trunk growth.

	Seasonal leaf growth	Mean leaf number	Leaf production (leaves·yr ⁻¹)	Leaf life span (mo)	Trunk growth (cm·yr ⁻¹)	Site
<i>Cibotium taiwanense</i> ^b	Yes	5	3	15, 26	-	Taiwan
<i>Cibotium chamissoi</i> ^c	?	4	3.5	11	3.0	Hawaii
<i>Alsophila salvinii</i> ^f	Yes	6	3	24	6.9	El Salvador
<i>Alsophila auneae</i> ^g	Yes	6	5	17	6.7	Jamaica
<i>Cyathea spinulosa</i> ^d	No	-	-	7.1	8.9	Japan
<i>Cyathea pinnula</i> ^a	No	6	-	-	10.4	Costa Rica
<i>Alsophila erinacea</i> ^a	No	4	-	-	13.6	Costa Rica
<i>Alsophila setosa</i> ^e	No	?	8.7	-	14.5	Brazil
<i>Sphaeropteris cooperi</i> ^c	?	15	30	6	15.4	Hawaii
<i>Alsophila firma</i> ^{h*}	Yes	5	5	10	17.1	Mexico
<i>Cyathea nigripes</i> ^{a*}	Yes	4	-	-	17.1	Costa Rica
<i>Alsophila polystichoides</i> ^{a*}	Yes	3	-	-	18.8	Costa Rica
<i>Cyathea delgadii</i> ^a	No	7	-	-	21.3	Costa Rica

^aBittner and Breckle (1995), ^b Chiou *et al.* (2001), ^c Durand and Goldstein (2001), ^d Nagano and Suzuki (2007), ^e Schmitt & Windisch (2006), ^f Seiler (1981, 1995), ^g Tanner (1983), ^h this study, *deciduous

In *A. firma* median size classes (3–5.5 m) tended to grow faster (Fig. 5), while plants of the largest size classes (> 6 m) slow down in their growth. Nagano and Suzuki (2007) observed the same growth pattern in *Cyathea spinulosa*, and assumed that for larger size classes vertical trunk growth becomes a disadvantage, because it increases the risk of break down. Tree ferns can build an adventitious root mantle at the stem base, which may partly fulfill the same function as secondary thickenings in angiosperm trees (Ogura, 1972), albeit less efficiently. We assume that vertical trunk growth is also limited by decreasing water conduction efficiency in larger individuals, providing one reason why each species may possess different height limits (e.g. *A. firma* 12 m (pers. obs.), *A. setosa* 5 m (Schmitt and Windisch, 2006), *Cyathea spinulosa* 5 m (Nagano and Suzuki, 2007)).

The deciduous leaf phenology of *A. firma* (as well as *A. polystichoides* and *Cyathea nigripes*; Bittner and Breckle, 1995) seems to have no negative effect on trunk growth, because it can store starch in the trunk before leaf fall (Feldman and Nardi, 1973) and recycle nutrients for the synchronous production of new leaves. The evergreen species *A. auneae* and *A. salvinii* possess slower growth rates although they do not have to struggle with a leafless period (Table 3).

We observed that most trunks of *A. firma* were spatially aggregated at the study site, and one fallen but still rooted individual formed several new lateral shoots. Conant (1983) mentioned that several species of *Alsophila* (*A. cuspidata* group) produce adventitious buds on stems which can form branches when the plant has fallen. Schmitt and Windisch (2005) reported caulinar branch formation of *Alsophila setosa* from Brazil. The capacity of tree fern species to ramify belowground has not been considered with regard to its

spatial distribution. Excavating three separate groups of trunks of *A. firma*, we found that in two cases the smaller trunk emerged as a lateral shoot of the taller trunk within a distance of 60 cm and 80 cm, respectively. Because excavation damages the plants, it is difficult to know how many of our studied trunks within 1 m distance have been lateral shoots or individual plants. Future experiments could address this question with molecular methods to distinguish between trunk growth and leaf phenology of clonal and single trunks, to detect significant growth differences among trunk size classes depending on the origin of the trunk, and to estimate the age of clonal groups of trunks.

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